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THE EFFECT OF LIGHT ON PLANT REPRODUCTION

G. Klebs

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In dealing with the influence of light on the lower plants, the author first deals with the asexual reproduction of various algae, especially zoospore formation. Reproduction of various bryophytes seems to call for intense light to convert the necessary nutrients to substances that activate the dormant "rudimentum", an invisible material carrier. It is suggested that light may also alter certain physical relationships within the cell (e.g. the vacuole pressure). It is demonstrated that leaf and spore protenema act altogether differently towards light, with the former producing moss buds 8 days after exposure to light and the latter, in 4-5 weeks. The author draws a definite relationship between intense light and the formation of sex organs in the lower plants.

Author

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Green plants live out their whole lives under the mighty dominion of light. It is an integral and indispensable factor in their nutrition and affects both the growth and the various motions of the plant as a whole and of its individual parts. It is apparent from the start, therefore, that the highest of plant functions, reproduction, is also in some way influenced by light. This notwithstanding, relatively few observations have so far been made in connection with this matter. The reason for this is that while the morphological aspects of reproduction have already been extensively scrutinized and catalogued, the physiology of the reproductive process in plants is still in its infancy. The brief but comprehensive paper of Möbius[1] represents a survey of all of

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[1] M. Möbius, "Which Conditions Stimulate the Flowering of Plants and Which Inhibit It?" Mededeeling. Proefstation "Midden-Java", 1892. Biologisches Centralblatt, No. 20/21 (1892).

*Numbers in the margin indicate pagination of the original foreign text.

the known facts regarding the effects of light on the flowering of plants. It is immediately evident from this cursory compendium how few trustworthy data on this question there really are.

Having for some time been concerned with the reproductive physiology of the lower plants, I should like here to deal briefly with the question of the influence of light thereon, reserving a more detailed presentation of my findings for discussion in connection with other phenomena in a later paper. Our first concern will be asexual reproduction which plays the principal role in /642 the propagation of many cryptogamous plants. The role of sexual reproduction lies chiefly in creating stable conditions to assure continued existence of the species in a hostile environment.

The asexual reproduction of many green algae occurs through the medium of zoospores produced in greater or lesser numbers by the mother cell. Examples of this type of reproduction are particularly abundant among the filiform algae. In studying whether light affects this process, and if so, in what degree, one obtains different results in accordance with the specific nature of the organism in question. The resolution of the question is not so simple a matter as may seem at first: many and varied experiments are required before a clear answer appears in each particular case. One is always obliged to take into account the effects of other external factors. Because of its role in the assimilation of carbon dioxide, light is an essential factor in nutrition, the latter being a prerequisite for all reproduction. Light is by far the most important source of heat, and as such represents a major influence on all phenomena of life. This implies that determination of the specific effect of light requires knowledge of nutritional processes and their dependence on temperature. Such knowledge in turn is obtainable only provided other factors, e.g., moisture and

nutrient salt content of the medium, oxygen availability, etc. are also taken into account.

There are at all events algae whose zoospore producing activity is hardly if at all, affected by light, while other factors such as temperature, chemical activity of the medium, etc., influence it considerably. This is, for example, the case with the single-celled Chlorococcum infusionum algae[1]. Regardless of whether the experiment is conducted in light or in constant darkness, transferring these algae to fresh water after a period of cultivation in a nutrient salt-rich medium in humid air under bright illumination results in the immediate production of zoospores. This is likewise the case with the filiform alga Ulothrix zonata[2], which forms large quantities of zoospores upon transfer from cool, agitated water into warmer and calmer water. In these and in similar instances, light participates in the process of nutrition only, and has no /643 direct influence on the process of zoospore formation. For this reason, we shall not delve into the matter further here.

Another group of algae seems to exhibit almost the same relationship to light as the above, producing zoospores with equal efficiency both under illumination and in darkness. Closer examination, however, reveals that light does indeed exercise an important influence on them, though this influence can be masked by other concomitantly operating factors. A clear example of that about which we are speaking is Vaucheria sessilis, a species of alga which I have already discussed elsewhere[3] without sufficient attention to its response to light.

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[1]Compare with Artari, "Studies on the Development and Taxonomy of Several Protococcoids", Inaugural Dissertation (Doctoral Thesis), 1892.

[2]Compare Dodel, "Ulothrix zonata", Pringsheim Jahrbuch, Vol. X.

[3]G. Klebs, "On the Physiology of Reproduction of Vaucheria sessilis", Verhandl. der Naturf. Gesellschaft, Basel, Vol. X.

Transferring Vaucheria from a humid air (cultivation) environment into water, from a nutrient salt-free fluid into clean water, or from agitated water into still water invariably leads to the formation of zoospores regardless of whether the algae are exposed to the normal succession of days and nights, are illuminated constantly, or kept in total darkness, Nonetheless, it can still be said that of all factors affecting zoospore formation, light is the most powerful and influential.

In the case of Vaucheria the mainfold effects of light are clearly distinguishable among themselves. A prerequisite in all experiments where a reliable result is desired is that well-nourished cultures be employed. In other words, studies must be conducted on Vaucheria which have been exposed to bright light in the presence of nutrient salts for a sufficiently long period. Once such a culture has been developed, it can be allowed to grow in darkness with a reduced level of nutrition for a period of several weeks. Zoospores are formed in abundance after 15 days and even three weeks of maintenance under such conditions. At ordinary room temperature zoospore formation requires two days, so that given a healthy culture, light as a factor in nutrition can hardly be said to be of any significance. The effect of temperature on the process was determined by me with the greatest possible accuracy. Zoospores form at temperatures lying within the interval 3-26°C. In contrast to the other familiar effects of temperature, e.g., on growth, the maximum intensity of zoospore formation is observed soon after one oversteps the lower limit of 3° or backtracks from the upper limit of 26° (provided other conditions favor the process). Generally speaking, a temperature of 5-12° is required for the process to begin; variation of the temperature between 12° and 26° seems, on the other hand to exercise no significant influence, so that Vaucheria cultures behave /644

similarly at an average temperature of 15° and at temperatures varying in the 12-26° range (provided all other conditions which might tend to intensify zoospore formation remain unchanged). Temperature as a specific influence therefore need not be taken into account regardless of whether experiments are conducted in a darkened room, under diffuse light, or in direct sunlight. The observed effect of a drop in light intensity on the process thus appears all the more surprising, The simplest experiment which shows this involves cutting down the illumination of the culture without altering any of the other factors. A large amount of zoospores is then produced with a high degree of certainty by a normal, healthy water culture. The experiment still works with older, almost sickly cultures, however. Complete darkness is not required; all that is necessary is a noticeable reduction in the previous level of illumination of the test culture. Daylight is unsuited to this type of experiment, since its natural variation in the course of the day allows no proper conclusion to be drawn about the magnitude of the intensity difference required for the initiation of zoospore formation. Use of an artificial light source affords a means of determining this magnitude with much greater precision. I should not like here to delve too deeply into matters of experimental procedure. Suffice it to say that in one series of experiments I employed a single Auer-type gas glow lamp, and two such lamps in a second series of experiments. Coupled with a gas flow meter and an Elster precision gas pressure regulator, these provided constant illumination day and night. A characteristic of the Auer lamps is that they yield a great deal of light in relation to gas consumption without giving off too much heat. Water cultures of Vaucheria were placed a distance of 25 cm away from the light source and kept there for several days. After I had satisfied myself that no zoospores formation had taken place, the

same cultures were placed 50 cm further away, so that the light intensity dropped to 1/9-th of its former level. This resulted in zoospore formation. With healthy, sensitive cultures the same result was obtainable by reducing the level of illumination to 1/4-th of its former value. Likewise successful were the experiments on Vaucheria cultures kept for a time at a distance of 50 cm from the light source and then moved 50 cm further away from it. In all these cases a drop in light intensity had the effect of inciting zoospore formation. After a time, one observes the halting of the process. Reinitiation occurs only upon a still greater drop in illumination intensity, e.g., upon placement of the culture in total darkness. At the same time, by placing the culture at a distance of 1 m from the light source (or, better yet, 1.5-2 m away from it), /645 or by exposing it to weak daylight, one can observe that low-intensity light as such has a favorable effect on zoospore formation, so that the process continues for a longer time. The reason behind this effect of light on the zoospore formation, as on other physiological processes, is unfortunately still a mystery. It is important to note, nonetheless, that the effect of light in the case of Vaucheria can only be indirect. The plant is able to reproduce asexually independently of light with the aid of ordinary nutrients. The effect produced by diminishing the light intensity might perhaps be due to alterations of other cell functions, e.g., nutrition and growth, in some as yet unknown way which clears the path for zoospore formation. In this view, we are dealing here with the so-called correlation phenomena which are of such great importance to the inner life of the cell. Another species of alga affords an example of the direct influence of light on zoospore formation. I am referring to Hydrodictyon utriculatum, a species which I studied previously. When a strong net of these algae has been cultivated at a favorable temperature in a nutrient salt-rich

medium under bright illumination, it exhibits a tendency toward very active zoospore production several days after it has been transferred into clean water, for example. Light is a definite factor in the process, which is retarded after just two days of maintenance in complete darkness. Nutrient deficiency is not in question here. It is much more probable that light is involved in some particular aspect of the process, e.g., in certain of the necessary chemical changes. It is important to note that under certain conditions (in the presence of 1% maltose and a constant temperature of about 26°) zoospores can be formed even in darkness, so that the presence of light required under normal conditions can sometimes be obviated. For this reason, the role played by light in the reproduction of Hydrodictyon is not as essential as in certain instances to be discussed below.

The above observations indicate that light is in varying degrees a factor in the asexual reproduction of algae, playing an important role indeed in a number of cases. Future studies along similar lines will undoubtedly uncover many facts of like nature.

Ranking one step above the algae in the plant kingdom are the bryophytes or mosses, which are characterized by their ability to reproduce asexually in the most varied ways. Therein lies the reason for the ubiquitousness of these plants. Well acquainted as we are with the morphology of their reproduction,/646 our ignorance of the effects of various external factors on the various forms this reproduction takes is almost total. Having for some years been involved in studies on this problem, I should like here merely to mention certain findings relating to the effects of light. Let us first consider the true mosses whose development is characterized by the fact that the spore formed in the moss capsule in germination exhibits an algae-like proembryo, the so-called

protonema. It's from this that the leafy sex-bearing moss plant springs through subsequent budding. This is very easily observable with the Funaria hygrometrica, a very widespread true moss whose germination has already been described by the famous bryologist W.Ph. Schimper (his studies were later added to by Müller-Thurgau. To investigate the question of the conditions under which the microbud is formed on the protonema, spores were planted in a dilute nutrient solution, on damp sand, tuff, etc. After several weeks under bright illumination a robustly growing, green protonema consisting of branching cell threads makes its appearance. The most essential factor in the appearance of moss buds is light, whose intensity cannot be allowed to drop below a certain level. If a 3-4 week old well-developed protonema is placed in semidarkness, e.g., in the darker portion of an otherwise well-lit room no moss buds appear on it; a similar protonema allowed to remain by the window yields an abundance of buds. The culture in the darker portion of the room continues to vegetate, assimilate, and grow, but is unable to reproduce. I have in my possession, for example, sterile protonema cultures over two years of age. Under normal conditions, the protonema of Funaria dies a few weeks after budding. We thus have before us an instance of a short-lived, transient structure which can go on living for a long time beyond its normal age if prevented from reaching its highest stage of development. A similar case also occurs among the algae (the fresh-water Batrachospermum). Sirodot showed that the spores of the algae form a proembryo from which the sex-bearing plant soon springs under normal conditions. This algal proembryo can also vegetate independently for long periods (resulting in its earlier identification as the separate genus Chantransia). Sirodot probably produced the robust and independent vegetation of the proembryo by depriving it of sufficient light. Once this supposition is confirmed

by experimental study, a close analogy will probably be found to exist between the behavior of the proembryo of mosses and that of Batrachospermum. Goebel[1] /647 has already indicated the possibility of such an analogy.

The most important question which faces us here is that of the manner whereby light works its effect. A three-week-old, well-nourished protonema contains a large quantity of the usual nutrient substances which enable it to continue living for a longer time in darkness. It is therefore not a lack of such materials that hinders budding in weaker light, which in fact permits a certain degree of continued nutrition. This leads us to suppose that the appearance of moss buds requires certain chemical processes which can only occur if sufficient light is available. In order to prevent misunderstanding, I should like to further clarify my hypothesis. Each protonema cell of and by itself possesses the ability to form a moss bud through lateral budding; this ability, in my opinion, is associated (in accordance with the views expressed by Nägeli, de Vries, et al.) with a characteristically organized, invisible material carrier which I shall refer to as the "rudimentum" ("Anlage"). This rudimentum is able to develop only upon realization within the cell of a whole set of conditions dependent in some definite way on the environmental factors involved here, the most important in addition to the availability of moisture and oxygen is the presence of the usual nutrients required by all plants. These are in part formed directly through the assimilation of carbon dioxide (to form carbohydrates) and partly through combination of the latter with nutrient salts likewise drawn from the environment. While these conditions are quite sufficient for the

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[1]See Goebel's interesting paper entitled "On the States of Young Plants", Flora, 1889.

growth and division of the protonema cells, something more is called for in the formation of moss buds. This additional factor is intense light which initiates chemical processes whereby nutrient substances are converted into other special substances, which in turn bring the dormant rudimentum into action. It is quite possible that light also alters certain physical relationships within the cell (e.g., the vacuole pressure) in the appropriate direction. But such effects would in the final analysis likewise be traceable to chemical, light-initiated processes.

The hypothesis I have just proposed is bolstered by certain other facts as well. It was W. Ph. Schimper who first reported that Funaria leaves cut from the mother plant and maintained under moist conditions are able to develop a protonema whence moss buds subsequently sprout. This finding is easily confirmed with the aid of dilute nutrient salt solutions. The question now /648 arises whether the leaf protonema has the same response to light as the spore protonema. Experiment yields the startling result that the leaf and spore protonemata have altogether different physiological properties. Even with good illumination, the latter produces moss buds only after 4-5 weeks, while the leaf protonema exhibits them after just eight days. Still more important is the fact the leaf protonema appears to be much more independent of light, yielding buds at a level of illumination at which the spore protonema remains completely sterile. Even in extremely weak light, in almost total darkness, the long, colorless, and almost unbranched threads of the leaf protonema develop isolated buds which remain undeveloped due to the lack of nutrients. These observations indicate that the cells of the leaves and moss stems contain precisely the substances necessary for moss bud formation, so that the leaf protonema is in a position to initiate the process immediately, while the spore

protonema acquires this ability only upon prolonged exposure to light. It is highly probable, however, that the substances in question are produced in the leaves only upon illumination.

The second class of bryophytes consists of the liverworts (Hepaticae) which differ from the leafy mosses in several important respects. In addition to the differences having to do with the development and structure of the spore capsules, the liverworts lack a developed protonema. The spores of many species exhibit a simple germ sac from whose tip the new moss plant emerges; other species have an occasionally branched cell thread which buds at one end. More distinctive still are such liverworts as Radula et al., whose spore forms a cell body which then becomes the bud[1]. According to the studies of Leitgeb[2], germination of liverwort spores is highly dependent on light. Light of medium intensity is generally most favorable, although a germ sac or thread may still form in weak light, only to die without budding. We might suppose from this /649 that by using the proper procedure one might obtain a sterile protonema as in the case of Funaria. Each spore of Jungermannia bicuspidata, porphyroleuca, et al. planted in a dilute nutrient solution and exposed to bright light after several weeks yielded a short-celled, somewhat branched thread. Before any sign of a moss bud had a chance to appear, the culture was placed under weak

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[1]It is only in very rare cases that liverworts have been known to have a highly developed protonema. Of great interest in this respect is Protocephalozia ephemeroides which was discovered by Spruce and discussed by Goebel. As in the case of the leafy moss Ephemerum, its protonema is more highly developed than the sex-bearing plants growing on it. See Goebel, "Studies on Archegonia", Flora, 1893.

[2]Leitgeb, "The Germination of Liverwort Spores and Its Relationship to Light", Sitzungsberichte der Winer Akademie, Vol. 74, 1876.

illumination, e.g., into the darker part of a room, as in the case of the leafy moss experiments. The small prothallium continued to grow slowly for a time and finally knotted up, remaining sterile and continuing to live. My own specimens have already been maintained alive in this way for over nine months and thus constitute exceptionally long-lived and highly developed liverwort protonemata. When exposed to bright light, the latter yield moss sprouts within a short time as do the leafy mosses. The conclusions drawn from studies of the leafy mosses also hold for the liverworts. This is further evidenced by an experiment on pruned leaves. Leaves of Lophocolea bidentata cultivated in bright light in a nutrient solution develop numerous buds from their border cells without previous formation of a protonema. The same experiment also succeeds when carried out in a weak light, in which the spore protonema remains sterile. I shall not discuss any further the numerous other phenomena involved in the asexual reproduction of leafy mosses and liverworts, pending the outcome of my present experiments. The cited observations are sufficiently strong testimony to the importance of light in moss reproduction. Future studies will undoubtedly show light to be equally significant in the asexual reproduction of the class of pteridophytes. I should like to point to one example of its influence on the reproduction of these plants remarkable for its dissimilarity to the case of the mosses. Several researchers (Hofmeister, Goebel, de Bary, et al.) have already found that the sexual generation of the ferns, the prothallium, has the ability to reproduce itself by way of the adventitious shoots emerging mainly from its border. My studies on numerous fern species indicate that light plays an important role in this process. If, for example, one plants spores of, let us say, Polypodium aureum in turf and sees to it that the developing prothallia are allowed to develop without obstruction, the result

obtained under bright illumination is that of the familiar heart-shaped leaves on which the sexual organs later appear. Upon being placed in a weak light (all other conditions remaining unchanged), the young turf cultures develop a large/650 number of adventitious shoots out of their border cells. These take the form of longer or shorter filaments, some of which tend to flatten out. Weak light is the decisive factor in bringing about this process, which fails to occur under intense illumination[1]. Much more lively and distinctive is the reproduction of Pteris cretica, whose germination was described by de Bary without special regard to the attendant conditions. Cultivation of both young and old prothallia of this species in nutrient solutions under weak light induces many of the border cells to develop into long cell threads which in turn branch out and finally form a protonema of similar thread mass. Only under intense light do the tips of these threads develop into flattish prothallia. The threads developed by Pteris resemble even more the thread prothallium of the fern genus Trichomanes. Goebel[2], in describing the peculiarities of the sexual generation, regards Trichomanes as the lowest form of fern and relates it directly to the simplest moss Buxbaumia.

As we broach the question of the influence of light on sexual reproduction, we note immediately that the problem here is much more difficult and complex than in the case of asexual reproduction, so that our total ignorance of the

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[1] I am not yet prepared to state categorically that no other factors play an essential role in inducing the process. At any rate, weak light is at present the simplest and most effective method of producing adventitious shoots.

[2] Goebel, "Studies on Archegonia. I," Flora, 1892.

relevant internal and external processes is quite understandable. In the majority of plants, sex organs appear as a matter of course; their appearance is a necessary step in the developmental process based on the inner laws of plant life. In the lower plants, on the other hand, sexual fertilization is a rather uncertain matter, and one is fortunate to observe it when it does occur. There can be no doubt, however, that external factors play a much more important role in sex organ formation in all plants than has heretofore been supposed. Many years of studies on this problem leave me firmly convinced that algae develop sexual organs under certain very special external conditions which occur in nature with greater or lesser frequency. Our immediate task is to determine the exact nature of these conditions. With this knowledge it should be possible to induce every species to reproduce sexually, even those for which this mode of reproduction is very rare. Among the external factors to be con- /650 sidered, light most certainly plays a very important role. Determining the degree and mechanism of its action is quite a difficult problem, however. The reason for this lies in the very extensively valid rule that the formation of sexual organs requires a large assembly of organic substances. The latter can and is achieved in many cases through the retardation of nutrient-consuming growth. As the practical experience of plant cultivators has shown, an inhibition of growth in many cases stimulates sexual activity. Along with this, however, a high level of nutrition is a prerequisite for the initiation of the sexual process. For this reason alone, light is a major factor in sexual reproduction. The more complex the structure of sex organs and the longer the time required for their development, the more difficult the recognition of the specific effects of light on this development.

The problem is simplest in the case of the lower algae, in which the

fertilization process requires just a few days. This, for example, is the case with Hydrodictyon utriculatum and its lively gametes which copulate to produce the resting cyst (zygote). The formation of the gametes is independent of light: they can be formed in the algal cells even after weeks of darkness provided the cells are kept supplied with an organic nutrient, e.g., cane sugar. Nevertheless, as with the zoospore formation of Vaucheria, a reduction of the intensity of light on a Hydrodictyon culture tends to stimulate gamete formation, so that the same culture can be made to reproduce both sexually and asexually simply by keeping one half brightly and the other half weakly illuminated. The role of light in this case appears to be the same as with Vaucheria. Provided other conditions are conducive to the process, reducing the intensity of the incident light retards growth and asexual reproduction and thereby stimulates gamete formation.

The effect of light on Vaucheria is much more direct. A well-nourished Vaucheria sessilis culture exhibits sex organs after a few days of exposure to bright light and no sex organs under weak illumination. The only effect achieved in weak light so far has been inducement to further development of sex organs which first appear under bright illumination. Placement of the culture in total darkness is not required: the dim light of a room is quite sufficient to inhibit sex organ formation without interruption of growth and nutrition. In this way it has been possible to maintain Vaucheria cultures sterile for several years, even though under normal conditions the plant dies after several /652 weeks of intense sexual reproduction. A lack of nutrients cannot be the cause of sterility in Vaucheria. No known organic substance has yet been found capable of fulfilling the function of light. We therefore conclude that, as with the mosses, the role of light in the process is a highly specific one. This

applies especially to the initial unfolding of the sex organ rudimentum ("Anlage") residing in every Vaucheria alga.

In all experiments with Vaucheria I saw to it that all of the other conditions required for sexual reproduction were present. The formation of sex organs by this alga can be inhibited in other ways, e.g., by keeping the culture at a low temperature of 0-3° while under bright illumination or by cultivation in running water. Reduction of light intensity is still the simplest and most sure way of producing the sexual sterilization of Vaucheria, however.

According to my later studies, other algae behave similarly to Vaucheria. The conjugation phenomena in Spirogyra Weberi, Closterium Lumula, and Cosmarium Botrytis, the formation of sex organs in Oedogonium diplandrum and other species are all related to bright light. It must be said, however, that the specific influence of light is not quite so distinguishable in all these cases, since all of the other conditions attendant upon the manner and degree of its influence have not been studied with sufficient thoroughness. I shall also forego discussion of the influence of light on the sexual reproduction of the mosses, even though it is easy to establish that such liverworts as Lunularia, Marchantia, and Pellia and leafy mosses such as Funaria and Barbula evidence inhibition of sex organ formation in dim light. This alone does not constitute adequate ground for drawing conclusions on the matter, however, since the formation of sex organs in the mosses requires more time, so that inhibition of this process may be due to deficient nutrition. The same may be said of my studies on the effects of light on the prothallia of ferns. Suffice it to say that I have succeeded in keeping the short-lived sexual generations of certain fern species alive and sterile for one year and longer by keeping them in dim light. It is my hope to discuss my findings with these plants in detail on a

future occasion.

Of very special interest is the problem of the role of light in the sexual reproduction of the phanerogamous plants. Although I myself have not yet performed any experiments on the latter, I should like to discuss the most important known facts in connection with the relationships prevailing in the case of the cryptogamous plants. Relatively few experimental studies have been published to supplement the many occasional and undecisive observations reported on this problem.

The most important results thus far available are those of Sachs[1], who /653 in his earliest studies showed that the bulbs of hyacinths, tulips, and Crocus grown in darkness yield quite normal blooms. Ashkenasy[2], who later preformed similar experiments, confirmed Sachs' results, though noting some loss of color with individual species (e.g., dark-blue hyacinths, Antirrhinum majus). With other plants such as Tropaeolum majus, Cheiranthus Cheiri, Cucurbita, on the other hand, Sachs noted a failure of the blooms to develop normally, although the sprouts grown in darkness continued to form vegetative organs. From this he concluded that it is the special quality of the formative substance and not its quantity which is decisive in flower formation. Sachs then proceeded to perform an extensive series of experiments involving exposure of the leafy part of the plant to light and placement of the top shoot in a dark container. Under these conditions the aforementioned species yielded both normal leaves and fruit in darkness. In the case of Cucurbita and Petunia, Sachs asserts

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[1] Sachs, "Collected Papers on Plant Physiology", 1892; the papers referred to originally appeared in 1863-1864.

[2] Ashkenasy, Botanische Zeitung, 1876.

that some of the flowers formed entirely in darkness through new growth. His experiments show conclusively that the leaves exposed to light assimilate all of the required formative substances, permitting normal blooming to occur in darkness. On the other hand, the results provide no clear indication whether and to what degree light exerts a specific influence on the formation of the special floral substances, leading Frank[1] (among others) to assert on the basis of precisely these experiments that flower growth occurs without regard to light or darkness.

Still less conclusive in this regard are the observations of other researchers. Kerner[2] reports, for example, that plants such as Epilobium angustifolium yield few flowers or none at all if kept in the shade. Kerner also noted that in general, leaf buds form on the shaded sides of plant stems, while flower buds form on the sides exposed to sunlight. Möbius performed several experiments in connection with this problem. He cultivated several types of plants such as Borago officinalis, Phalaris canariensis, and Andropogon Ischaemum in pots, sunning and watering the first group, sunning and not watering the second, shading and watering the third, and shading and not watering the /654 fourth. His results indicated both dryness and light to be decisive influences. The observations of Möbius and others indicate that for most plants,bright light stimulates blooming. The data available so far do not permit us to identify and distinguish between the specific effects of light, however.

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[1] Frank, "Textbook of Botany", Vol. I, 1892.

[2] Kerner, "Plant Life", Vol. II, p. 388.

The experiments of Sachs[1] involving the use of light deprived of its ultraviolet rays are significant in this regard. Sachs cultivated Tropaeolum majus plants in closed boxes with one glass cell side through which all of the light made available to the plant had to pass. The glass cell of one box was filled with water; the others contained a quinine sulfate solution for filtering out the ultraviolet rays by transforming them into low-refrangibility rays through fluorescence. The plants behind these cells received only ultraviolet-deprived light of the same brightness as that received by the control plant behind the water-filled cell. The experiment, which lasted several years, showed that the Tropaeolum plants behind the water-filled cell yielded an abundance of flowers, while those behind the quinine solution ceased to bloom almost completely. Thus, Sachs reports that while 20 plants behind water-filled cells produced 56 flowers, 26 plants behind the quinine cells yielded but a single sickly flower. Casimir de Candolle[2] obtained similar results in his experiments. His studies on Lobelia Erinus grown behind an esculin solution with fluorescent properties similar to those of quinine yielded results not quite so definite, however.

The influence of ultraviolet light on flower formation observed by Sachs is of great interest indeed. His finding represents the first proven indication of the role of light in the reproduction of flowering plants, but the manner and time in which ultraviolet rays affect the flowering of Tropaeolum remains a mystery. Sachs hopes by the experiments just described to confirm

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[1] Sachs, Arbeiten des Würzburger Instituts, Vol. III, 1886; see also his "Collected Papers", Vol. I.

[2] C. de Candolle, "Etude sur l'action des rayons ultraviolets sur la formation des fleurs", Archives des scienc. phys. et nat., Vol. 28, 1892.

his earlier hypothesis about the factors involved in structural development. In his view, ultraviolet rays participate in the formation of minute amounts /655 of substances other than the usual nutrients, which, upon arriving at the sites of vegetation, act similarly to enzymes to transform nutrients and produce flowers. In this postulation of such unstructured and yet structure-forming flower enzymes, Sachs stands in sharp opposition to the ever more commonly held view, to whose advancement I have myself contributed, that the structure of flowers originates at rudimentum ("Anlage") already residing at the point of vegetation. In no sense do Sachs' experimental results resolve this fundamental and well-nigh irresolvable issue, for what is involved here are two very preliminary and purely theoretical hypotheses. The experiments on Tropaeolum can perhaps be treated in the same way as I did above in the case of the cryptogamous plants. The assumption can be made that the unfolding of the rudimenta of reproductive organs (whatever form these may take) requires chemical processes different from the usual processes of nutrition, and that these special processes are in many cases dependent on light.

It would be very valuable indeed to extend Sachs' experiments to other plants in order to determine the general applicability of his results. Sachs himself notes that the chlorophyll-free parasites can bloom in total darkness, and therefore claims validity for his conclusions in the case of green plants only. I was myself interested in determining how the cryptogamous plants I studied behave in this regard. It is my firm conclusion that it is the intensity of light which plays the decisive role in every case where reproductive phenomena exhibit any dependence on light whatever. This aspect of the problem is not touched on at all in Sachs' papers. Provided the incident light was of sufficient intensity, I found that Vaucheria sessilis finally produces sex

organs whatever the wavelength of this light, from red all the way to ultraviolet. It appears in general, however, that the blue-violet half of the spectrum is more important to the process than the red-yellow half. It turns out that sex organs form more slowly behind a picric acid solution (clear to the eye) than behind a solution of copper ammoniate (almost opaque). Filtering of light through a quinine solution, on the other hand, seems to have no appreciable effect on the rate of sex organ formation in most cases.

The above survey of information available to us about the effects of light on the reproduction of plants, despite the general dearth of solid fact, demonstrates clearly the great importance of light in this highest function of /656 the plant organism. It cannot be disputed that studies in this area will form an essential part of the physiology of reproduction in the future.

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